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RESEARCH ARTICLE
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Surface Stability in Drylands Is Influenced by Dispersal Strategy of Soil Bacteria

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Key Points:
- Microbial communities of dryland ephemeral lake bed, dunes, and river channels are characterized
- Wind preferentially mobilizes specific microbes from soil surface biocrusts
- Microbial dispersal adaptations may influence soil stability by promoting or inhibiting adhesion

Supporting Information:
- Supporting Information S1
- Text S1
- Table S1
- Table S2
- Table S3
- Data Set S1
- Data Set S2
- Data Set S3
- Figure S1
- Figure S2

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Abstract Microbial adaptations for survival and dispersal may directly influence landscape stability and potential for dust emission in drylands where biological soil crusts (biocrusts) protect mineral soil surfaces from wind erosion. In the Lake Eyre basin of central Australia we operated a wind tunnel on sandy soils and collected the liberated material, which was subjected to DNA sequencing to identify the microbial community composition. Microbial composition of entrained dust was compared with that of the source sand dune soil in addition to nearby claypan and nebkha soils and water channels that together form a recycling sediment transport system. Wind was found to preferentially liberate 359 identified taxa from sand dunes, whereas 137 identified taxa were found to resist wind erosion. Water channel communities included many taxa in common with the soil samples. We hypothesize that the ease with which soil microbes become airborne is often linked to whether the organism is adapted for dispersal by wind or vegetative growth and that biocrust organisms found in water channels may sometimes use a fluvial dispersal strategy, which exploits rare flooding events to rapidly colonize vast pans that are common in drylands. We explain likely geomorphic implications of microbial dispersal strategies which are a consequence of organisms engineering the environment to provide their particular needs. By identifying microbes fitting expectations for these dispersal strategies based on differential abundance analyses, we provide a new perspective for understanding the role of microbiota in landscape stability.

1. Introduction

In drylands where vegetation is sparse, soil microbes provide some ecosystem functions that are normally delivered by plants in temperate vegetated systems (e.g., Lange et al., 1992; Ferrenberg et al., 2017). Microbes in the soil surface of drylands form biological soil crusts (biocrusts), which reduce erodibility by wind and water (Eldridge & Leys, 2003; Liu et al., 2017), fix carbon and nitrogen (Li et al., 2012; Büdel et al., 2018), alter the surface albedo, and increase water holding capacity (Singh et al., 2016; Adessi et al., 2018). Biocrusts were among the first organisms to colonize land (Beraldi-Campesi, 2013); therefore, it is to be expected that they are well adapted to both exploit soil surface conditions and modify their environment for their own advantage. By identifying and understanding the adaptations of biocrust organisms, we can gain insights into the biotic forces that influence geomorphic processes. In this paper we investigate how individual microbial taxa contribute to soil stability in western Queensland, Australia, and relate this to their hypothesized ecological strategies for survival.

The interactions between fluvial and aeolian processes in drylands have been demonstrated as important over timescales ranging from seasons to glacial-interglacial cycles (McTainsh, 1987; Langford, 1989; Bullard & McTainsh, 2003; Field et al., 2009). Fluvial systems can deliver large quantities of sediment downstream within catchments that, once deposited and desiccated, are susceptible to wind erosion. The combination of water flow and wind direction can result in sediment cycling at a range of different spatial scales from catchments exceeding 1×10^6 km^2 (Bullard & McTainsh, 2003) to within smaller dune-pan systems (Thomas et al., 1993). Microbiota have not generally been considered as a component of this fluvial-aeolian system; however, it has been recognized that biocrust organisms can act as ecosystem engineers (Viles, 2008).

In this paper we report on the microbial ecology of a dynamic ecosystem in central Australia comprising a 25-km^2 claypan in the Lake Eyre basin bounded by sand dunes and ephemeral river channels, where

fluvial-aeolian interactions are thought to have been occurring at least since the Last Glacial Maximum about 10 ka BP (Bullard & McTainsh, 2003). To provide insights into how biocrust microbial ecology affects soil stability, we determined the microbial composition of different dryland soils and sediments and then identified possible ecological strategies (especially dispersal mechanisms) of the microbes present. As microbes were expected to be dispersed by both air and water, we also analyzed the microbial composition of nearby river channels and airborne dust liberated by in situ wind tunnel treatment on sand dunes. By developing understanding about the ecology of dryland soil microbial communities and their constituent individual taxa, it should be possible to predict biological responses for various scenarios and devise interventions to manipulate the biotic component of geomorphic processes. This would have a wide range of potential applications in land management, for example, to enhance carbon storage, suppress dust emissions, and make predictions of future geomorphic activity under a changing climate. By comparing the microbial composition of different system parts we evaluated possible dispersal strategies of individual taxa and interpreted these findings in relation to soil stability and dust emissions.

There are a limited number of studies on the microbial content of airborne sediments (Acosta-Martinez et al., 2015), most of which focus on long-distance transport of pathogens relevant to human health. Studies with a more environmental focus that have looked at the microbiota found naturally within major dust sources or in the air near to known dust sources in Australia include De Deckker et al. (2008), Lim et al. (2011), Abed et al. (2012), and Munday et al. (2016). These studies have characterized microbial communities in aerosols and dust sources, highlighting the possibility of nutrient transportation along with microbiota and demonstrating potential applications of microbiome science for tracing dust to its source. The authors of all of these papers pointed out that due to mixing in the air, it was not possible from their data to relate the airborne microbiome directly to any specific source. The only previous study utilizing a wind tunnel to collect airborne particles and microbes is Gardner et al. (2012), which used a pyrosequencing approach to determine the association of particular microbes and diversity metrics with organic matter and particle size fractions. Prior to wind tunnel treatments the soils in Gardner et al. (2012) were tilled, raked, and flattened using a lawn roller, in contrast to the present study which used soils in their natural condition. Due to our methodology employing a wind tunnel we were able for the first time to unequivocally collect and analyze wind-eroded microbiota from a specific known natural source.

Our main hypotheses are that different compartments in fluvial-aeolian systems harbor distinctive microbial communities and that wind erosion selectively mobilizes certain taxa from biocrusts. We expect this because it is known that biocrusts stabilize dryland soils, and this stability is clearly linked to the survival prospects for biocrust organisms because shifting soils will prevent the establishment and succession of biocrusts (e.g., Felde et al., 2018). So while we expect a strong selective pressure in biocrust organisms for promotion of soil stability, it should be recognized that this is a benefit to the community not just the individual taxa investing considerable resource to stabilize the soil. If some biocrust organisms are exploiting community resources rather than contributing to biocrust survival, then it can be further hypothesized that such taxa may reduce soil stability and contribute to dust emissions. If this is the case then one might expect these organisms to be adapted for aerial dispersal via liberated dust so that they can rapidly find new crusted surfaces to exploit after depleting resources in a particular location.

2. Methods

2.1. Field Site and Sampling

Work was carried out at Diamantina National Park in western Queensland, Australia (23°36′44.8″S; 143°17′46.9″E). Climate in the region is semiarid and characterized by a summer-dominant rainfall pattern with a mean annual precipitation of 270 mm/a and high interannual variation. Central to the study site is 25 km^2 of claypan, bordered by sand dunes and multiple channels of the Diamantina River. Aeolian activity moves sediment from the dunes and claypan, while periodic flooding (interval ~3 years) brings fresh river sediment to the claypan (Figure 1). A linear dune runs approximately north-south on the west side of the claypan, and this was the location from which sampling transects were established (Figure 1). Soil was sampled from five transects perpendicular to the dune, and water/sediment was sampled from water channels in the surrounding area. Transects were ~500 m apart along the dune extending into the claypan. Some zones to the south were impacted by unauthorized cattle trampling, and these areas were avoided. The transects are numbered 1–5 starting at the south end.

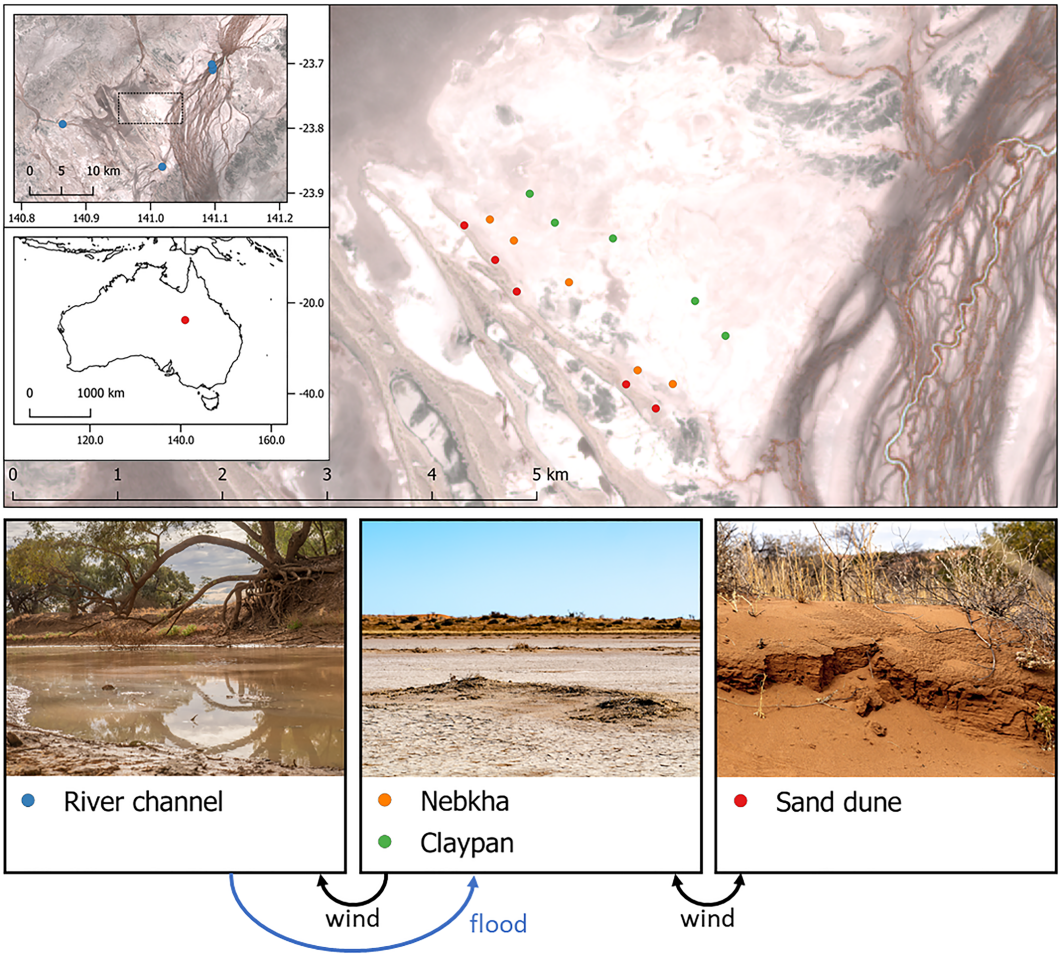

Figure 1. Aerial view of sampling locations with identification of sample types and illustrating the position of transects in the landscape. Insets show site position within Australia and the general area of claypan including surrounding water channels. Main image shows a closer view of dune and pan area. Lower panels show photographs of the main system compartments, with markers keyed to match with aerial imagery. Arrows illustrate expected linkages between system components by aeolian and hydrological transfer of sediment and inoculum. Aerial imagery from Copernicus Sentinel 2 data (2015).

The following locations were targeted for soil sampling (See Figure 1, Figure S1 in the supporting information for photographs, and Table S1 for coordinates):

D. Dune. Dune biocrust.
DF. Dune Flank. Dune flank biocrust. These sites were also used for wind tunnel experiments.
P. Pan. Biocrust platelets in vegetation interspaces on the claypan (there is very little vegetation on the claypan).
N. Nebkha. Biocrust situated on nebkha in the claypan to the east of the dune.
C. River channel. Sediment and water from the banks of water channels surrounding the dune/claypan complex.

The dunes were characterized by coarse sand-textured bare crests with frequent sand movement. Vegetation, biological crusts, and soil texture progressively change moving down the middle to lower flanks stabilizing the surface. Shrubs (e.g., *Acacia bivenosa*, *Rhagodia* spp.) and grasses (e.g., *Zygochloa paradoxa*) appear across the dune flanks with a high level of spatial heterogeneity. Surface sediments begin to be stabilized by an extensive cover of cyanobacterial crusts from the upper middle slopes, becoming strong by the lower flanks. These contribute, along with the increased finer texture (loamy sand), to low soil surface roughness, typically up to 7-mm amplitude across a meter length and commonly comprising a coarse sand layer atop of a smooth cyanobacterial crust. The seasonal conditions amplified large open areas with limited annual

vegetation growth. This facilitated easy site selection away from perennial shrubs and grasses to perform the crust sampling. Importantly, this minimized possible influence of vegetation on soil cohesion and microbial community structure.

Biocrusts on the claypan typically have a blue-green appearance due to the presence of photosynthetic organisms and have a platelet formation caused by physical weathering (Figure S1). They appear to have once been widespread but had been largely eroded away at the time of sampling in July 2015. Underneath claypan platelet crusts was a brown colored crust, and this was not sampled in the present study. In many places on the claypan there were small nebkha dunes, and the crust platelets encroached up the nebkha flanks.

The sampled nebkhas followed the dune orientation and were all on the northeast flank (side) of the NW-SE trending dune. Each nebkha sampled had a low, broad, well-rounded profile of heights less than 10 cm. The vegetation elements, which are important in the capture and stabilization of sediment, were at the time of sampling desiccated providing very limited solar protection and probably very little in terms of productivity. Residual vegetation elements still present included forbs belonging to *Sclerolaena* sp. and *Portulaca* sp. Despite the desiccated nature of the vegetation, biocrust sampling from each nebkha was performed away from the vegetation to minimize possible influence. Biocrusts were consistently sampled from the nebkha margin where the ground became raised compared to the surrounding flat pan. There were visible differences between biocrusts on these nebkha mound edges and the surround pan surfaces.

For soils the sampled areas were 10 × 10 cm and were selected to represent the diversity of biocrust in the area (see Figure S2 for photographs). The sampled depth of ~5 mm was dictated by natural coherence of the biocrust. The area was cut out with a sterile scalpel and the crust was lifted off the unconsolidated soil beneath. In areas where differing crust morphologies were noticeable, the sampled areas were selected to have both types where applicable. Water channels were sampled by dragging a 5-ml sterile bijoux along the bank where it meets the water. Approximately 2.5 ml bank sediment and 2.5 ml standing water were collected in each bottle from the same location.

2.2. Wind Tunnel

A wind tunnel was run on dune flanks within 3 m of where the soil crust was sampled for the dune flank samples. The wind tunnel was a duct-type design equipped with a sediment collection trap in which sterile filter papers were fitted. Further details of design and operation have previously been described by Strong et al. (2016). The wind tunnel was run on dune flanks because they are relatively flat, and being naturally eroded by saltation impact from the dune sand above during windy conditions, they likely act as an inoculum source to surrounding areas more so than the higher dune areas. At each site the wind tunnel was run 3 times on adjacent areas for 5 min at 10 m/s for 5 min. This is a moderate treatment intended to be realistic and to collect only the easily mobilized particles/organisms.

2.3. Soil Properties

Total carbon and nitrogen content of soils were determined using a CN element analyzer (Leco TruSpec). Particle size distribution was determined using a Beckman-Coulter LS280 laser-sizer in the range 0.375–2,000 μm with 93 class intervals. Soil pH was determined using a Sartorius PY-P10 probe after mixing soil in water according to the method of Rowell (1994), scaled down for small samples.

2.4. DNA Sequencing

DNA was extracted in the field within 24 hr of sample collection using a Mobio Powersoil DNA extraction kit according to the manufacturers instructions except for increasing the soil amount slightly to 0.4 g per sample as described previously (Elliott et al., 2014). DNA sequencing targeted the prokaryotic 16S rRNA gene v4 region and was performed by the Centre for Genomic Research (CGR) NERC Facility at the University of Liverpool, using an Illumina MiSeq in a Paired end approach (2 × 250 using v2 reagents). The primer design, PCR, and barcoding approach followed the method of Caporaso et al. (2011) using primers 515F and 806R (15 cycles) for amplification of v4 region, then a second nested PCR (15 cycles) to incorporate illumina adapter sequences and barcodes. Barcodes were as described in the Illumina Nextera protocol.

2.5. Bioinformatics

FastQ files from DNA sequencing were processed using VSEARCH v2.8.4 (Rognes et al., 2016) for quality control and clustering of reads into operational taxonomic units (OTUs). Parameters included maximum expected error rate of 0.25 for stringent sequencing error rejection, denovo chimera removal followed by reference-based chimera removal using the Gold database (Haas et al., 2011), and denovo clustering of OTUs

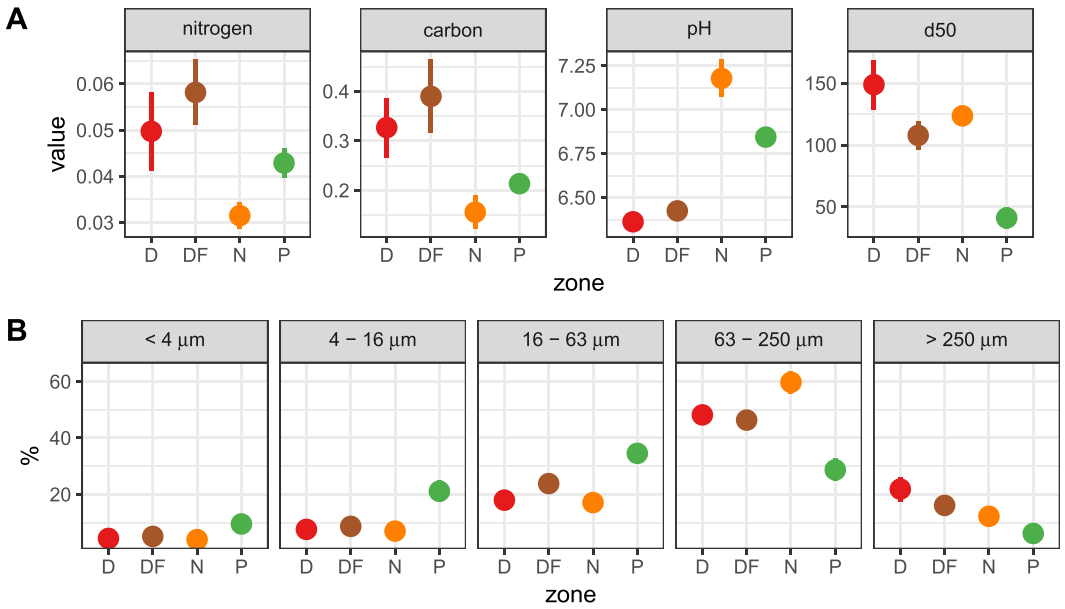

Figure 2. Soil properties in and around Lake Constance claypan at Diamantina National Park, Australia. (a) Mean total carbon and nitrogen (% w/w), pH, and particle mass median diameter (µm); (b) particle size distribution. Error bars represent the standard error of the mean for each soil type (n = 5). Sample coding for soil types: D = sand dune, DF = dune flank, N = nebkha, P = pan surface.

at 97 % similarity which typically approximates to species-level differences (Stackebrandt & Goebel, 1994). Taxonomy was assigned using UCLUST v1.2.22 (Edgar, 2010) as implemented in QIIME (Caporaso et al., 2010), using the SILVA database release 132 (Quast et al., 2013).

2.6. Statistical Analyses

OTU tables with assigned taxonomy from the bioinformatics pipeline were analyzed using R v3.5.1 (R Core Team, 2018) with packages phyloseq v1.24.2 (McMurdie & Holmes, 2013) and vegan v2.5-2 (Oksanen et al., 2018). Sequences identified as originating from chloroplasts or mitochondria were removed. Microbial community structure was visualized with respect to sample source using nonmetric multidimensional scaling (NMDS) based on Bray-Curtis dissimilarity calculated from relative abundance of OTUs. In the resultant NMDS plots showing the first two dimensions of the multidimensional space, samples with similar community composition are placed closer together (Kruskal, 1964). Possible correlation of measured variables with microbial community structure was evaluated by stepwise model building to select explanatory variables in a redundancy analysis (RDA), and using analysis of variance to test significance of selected variables to the model. All measured variables were used in this process including pH, C, N, and a range of particle size parameters (variables are available in Table S1 in the supporting information). Alpha diversity was evaluated by calculating the Shannon diversity index for each sample.

To identify OTUs with different relative abundance in the wind tunnel collection filter compared to the source dune flank soil, we used the model-based DESeq2 approach (Love et al., 2014) on nonrarefied reads as implemented in the phyloseq package. The DESeq2 method includes correction for multiple testing and is highly efficient on data preservation because it eliminates the need to perform rarefaction or normalization of count data (McMurdie & Holmes, 2014).

3. Results

3.1. Soil Properties

All soils and sediment samples contained low concentrations of carbon and nitrogen at below 1 % and 0.1 % w/w, respectively (Figure 2). Dune and dune flank sites contained approximately double the amount of carbon (mean 0.36 % w/w) compared to nebkha and pan sites (mean 0.18 %). Nitrogen levels were also slightly higher in the dune and dune flank sites (mean 0.05 % w/w) compared to nebkha and pan sites (mean 0.04 % w/w). The pH of dune and dune flank sites were similar at pH 6.4 whereas pan and nebkha sites were around pH 7.0.

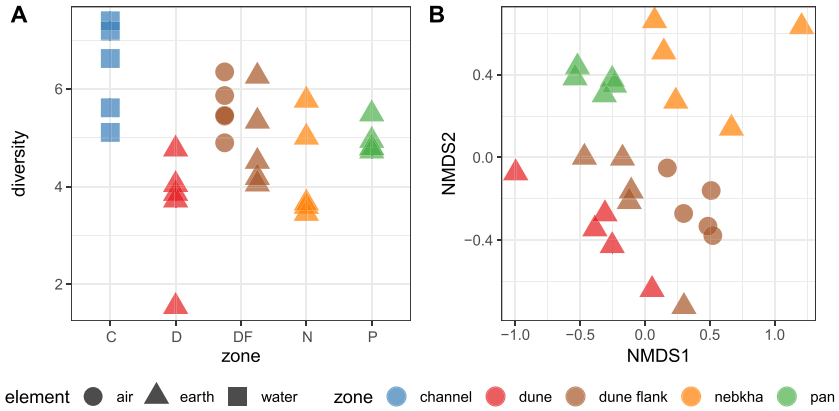

Figure 3. Prokaryotic microbial community diversity of soil (sand dunes, claypan, and nebkha), water channels, and airborne dust (from sand dunes). (a) Shannon diversity index (alpha diversity); (b) NMDS visualization of community structure (beta diversity). Water channel data are not shown on the NMDS plot because of extreme dissimilarity to other samples. NMDS = nonmetric multidimensional scaling.

Dune and dune flank sediments had similar particle size distribution, dominated by very fine to fine sands (46–48 %) with the modal particle size in the range 185–270 μm. The dune sediments were slightly coarser overall containing a higher percentage of medium and coarse sands and lower percentages of silt and clay than the dune flank (Figure 2). Nebkha sediments were also dominated by very fine to fine sands (60 %; mode 169–185 μm) and were well sorted. Pan sediments were less well sorted than any of the sites dominated by wind-blown material. The pan sites included the highest proportion of clay (~10 %) and silts (55 % total) and lowest percentage of sand-sized material (<35 %).

3.2. DNA Sequencing and General Microbial Community Composition

DNA was successfully extracted and sequenced from 30 samples, yielding 18.5 million reads. After pairing reads and quality control, 2.1 million bacterial reads and 20 thousand archaeal reads remained.

There were 17,913 bacterial OTUs and 107 archael OTUs detected (OTUs defined by 97 % similarity). This analysis was designed to target bacteria, and as archaea make up only 0.9 % of sequences, bacteria are the main focus of this paper; however, archaeal reads were retained for the analyses. The Shannon diversity index (Figure 3a) indicated similar diversity among all soil types including the particles eroded from the dune flank by wind tunnel treatment.

Initial visualization of microbial community structure by NMDS (Figure S3) showed that the water samples differed extremely compared to all other samples, and this dominated all other intersample differences. The water samples were therefore excluded from the NMDS to reveal the community structure relationships between the soil and airborne dust samples as shown in Figure 3b. Microbial composition of the dune, pan, and nebkha sites differed markedly. The airborne dust community derived from wind tunnel treatment on the dune flank differs from both the dune and dune flank communities, notably having a community structure approximately intermediate between the dune and nebkha communities.

High abundance OTUs are likely to be important contributors to the overall community differences (Figure 3), and many of the abundant OTUs were related to each other (Table S4), meaning that community differences may be evident and easier to understand at higher taxonomic ranks as shown in Figures 4 and 5. A total of 55 bacterial phyla and 6 archael phyla were identified. Frequencies of the most abundant phyla are shown in Figure 4 and are provided in full in Table S2. It can be seen that water channel samples are dissimilar to the soil-based samples at the phylum level although all abundant phyla (>1 % overall) are represented in both soil and water, except Deinococcus-Thermus which was not found in water channels. Cyanobacteria numerically dominated at the soil sites and were also common in river channels but much less abundant (overall Cyanobacteria accounted for 39 % of prokaryotic sequences). The numerically dominant cyanobacterial genus was *Microcoleus,* which accounted for over 8 % of sequences detected in all soil types (Figure 5). Several of the common cyanobacterial genera exhibited different abundance in relation to sample type, notably *Microcoleus* and *Trichocoleus* more common in dunes, and *Tychonema* more common

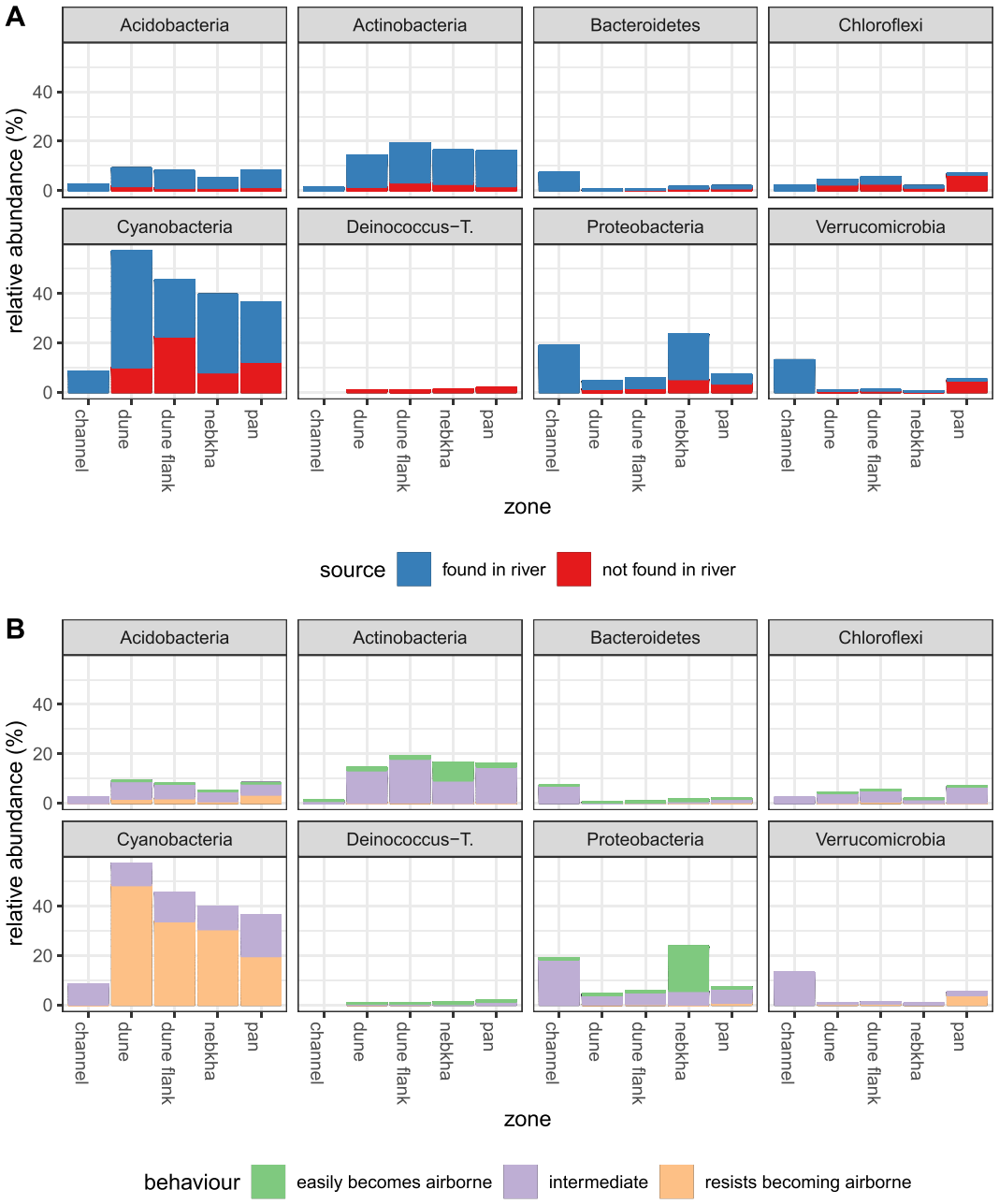

Figure 4. Relative abundance of identified bacterial phyla. Coloring indicates whether individual operational taxonomic units (OTUs; 97 % similarity) contributing to the phylum abundance were found in the water channels (a) and whether they were significantly more abundant in soil or wind tunnel collectors at the dune flank sites (b). Taxonomy of contributing OTUs and statistical results are provided in Table 1. Only phyla exceeding 1 % of total reads after quality control are shown for clarity (full data are provided in Table S2). Source designation is not indicative of the ultimate origin of OTUs.

in nebkha. In the river channels Proteobacteria and Verrucomicrobia were numerically dominant but only by a small margin and with several other phyla also common.

3.3. Correlation Between Measured Variables and Microbial Community Structure

A stepwise model building approach was used to identify measured variables which may explain microbial community structure. Only the particle size d50 (mass median diameter) had a significant correlation with microbial community structure ($p = 0.005$). The mass median diameter was negatively correlated with axis RDA1 in the resultant model (supporting information Figure S4), which indicates that the smallest particle

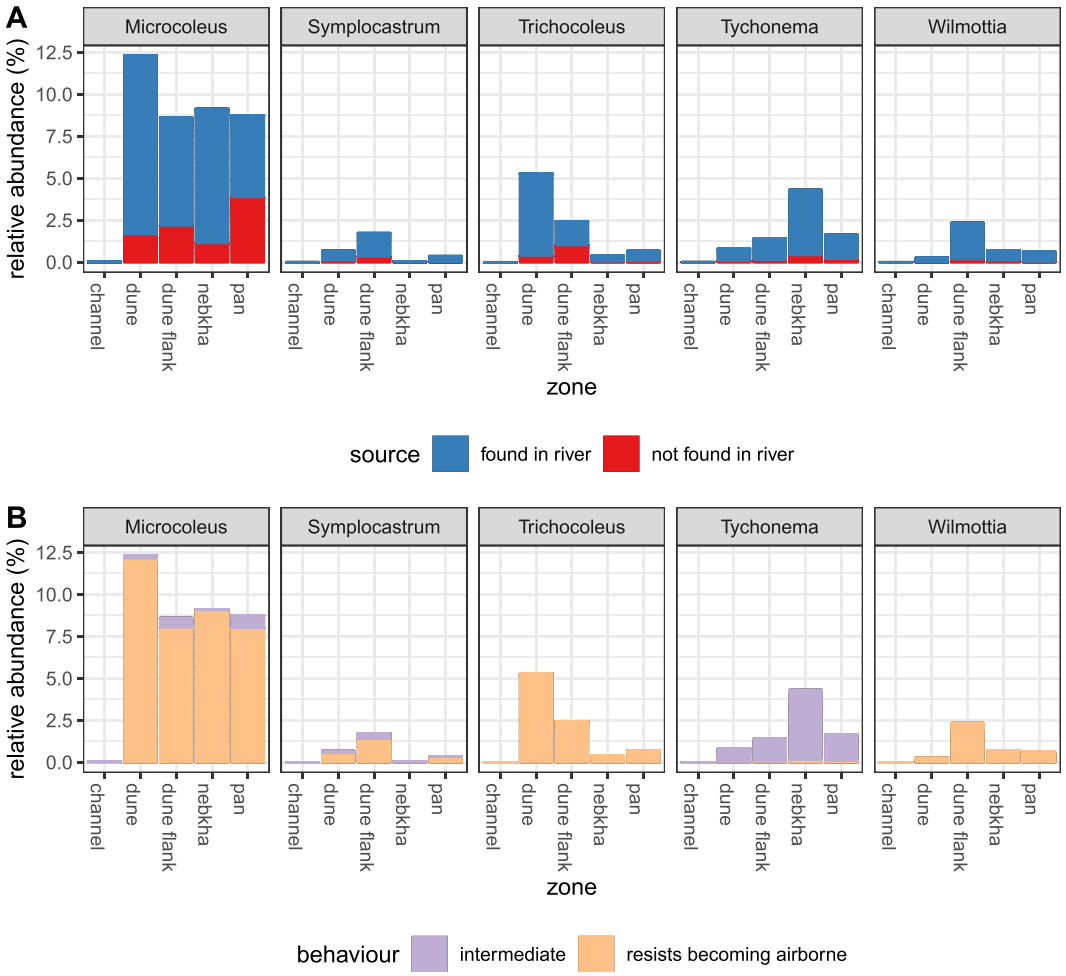

Figure 5. Relative abundance of identified cyanobacterial genera. Coloring indicates whether individual operational taxonomic units (OTUs; 97 % similarity) contributing to the genus abundance were found in the water channels (a) and whether they were significantly more abundant in soil or wind tunnel collectors at the dune flank sites (b). Only cyanobacterial genera exceeding 1 % of total reads after quality control are shown for clarity (full data are provided in Table S3). Source designation is not indicative of the ultimate origin of OTUs.

diameters were associated with pan communities, but other sample types did not clearly partition in relation to d50/RDA1.

3.4. Dispersal of Microbes by Fluvial and Aeolian Processes

Of the 3,548 OTUs found in the claypan, 451 were also found in water channels, 2,250 were found in airborne dust from the dune flank, and 392 were found in both. The dune and channel samples had 745 OTUs in common. While many soil OTUs were not detected in the air or water samples, most of the OTUs found exclusively in soil were rare, collectively accounting for only 4.4 % of reads in the soil samples.

OTU differential abundance analysis indicated that 359 OTUs (27 % of reads) were more abundant in air samples and 137 OTUs (36 % of reads) were more abundant in soil samples (adjusted $p < 0.05$). Details for a subset of these OTUs are shown in Tables 1 and 2 (extended results provided in Table S4). Results from these analyses were used to color code Figures 4 and 5 to indicate whether taxa easily become airborne under moderate windy conditions or not. It can be seen from these figures that some phyla and particular cyanobacterial genera differed in abundance between the dune flank soil and airborne dust liberated from the same soil by wind tunnel treatment. For example, phylum Cyanobacteria was more abundant in soil (resist becoming airborne) and phylum Deinococcus-Thermus was more abundant in airborne dust (easily become airborne). Further detail of cyanobacterial distribution given in Figure 5 shows that the most common cyanobacteria in the biocrust are from the genus *Microcoleus* and that most of these resist becoming

Table 1
Relative Abundance of OTUs Which Are Significantly More Abundant in Soil Compared to Dust Blown From the Soil

Phylum	Family	Genus	padj	Air (%)	Earth (%)
Cyanobacteria	*Coleofasciculaceae*	*Microcoleus*	0.00	0.11	2.91
Cyanobacteria	*Coleofasciculaceae*	*Wilmottia*	0.02	0.08	2.02
Cyanobacteria	*Coleofasciculaceae*	*Microcoleus*	0.01	0.04	1.76
Cyanobacteria	*Phormidiaceae*	*Trichocoleus*	0.00	0.06	1.38
Cyanobacteria	*Coleofasciculaceae*	*Symplocastrum*	0.04	0.30	1.36
Cyanobacteria	*Coleofasciculaceae*	*Microcoleus*	0.00	0.04	0.92
Acidobacteria	*Blastocatellaceae*	*Blastocatella*	0.00	0.12	0.72
Acidobacteria	*Pyrinomonadaceae*	RB41	0.01	0.16	0.69
Cyanobacteria	*Coleofasciculaceae*	*Microcoleus*	0.00	0.01	0.54
Cyanobacteria	*Coleofasciculaceae*	*Microcoleus*	0.00	0.02	0.54

Note. This is a subset of the differential abundance analysis output, sorted by magnitude of difference in abundance and excluding operational taxonomic units (OTUs) lacking genus level taxonomy information. The padj column indicates the probability of the observed distribution including adjustment for multiple testing. Multiple entries of the same genus means that multiple OTUs (approximately species level) within the genus met the criteria for inclusion in the table. OTU IDs and extended results are provided in Table S4 in the supporting information.

airborne. Other cyanobacterial genera exhibited similar patterns except for *Tychonema* OTUs which were not significantly more abundant in either soil or airborne dust (thus classified as intermediate behavior). Figures 4 and 5 also show the relative proportions of phyla and cyanobacterial genera which were detected in the water channels situated ~10 km from the dune sites. While nondetection does not signify that OTUs are certainly absent from water channels, it does show that they are exceedingly rare. OTUs belonging to phylum Deinococcus-Thermus were notably absent from river channels (zero observations) while comprising ~1 % of all reads (26,687 observations) at other sites. Cyanobacterial OTUs were also underrepresented in river channels compared to other phyla, especially those belonging to the genus *Microcoleus*.

Table 2
Relative Abundance of OTUs Which Are Significantly More Abundant in Dust Blown From the Soil Compared to the Whole Soil

Phylum	Family	Genus	padj	Air (%)	Earth (%)
Proteobacteria	*Burkholderiaceae*	*Massilia*	0.00	2.57	0.02
Actinobacteria	*Geodermatophilaceae*	*Modestobacter*	0.01	1.47	0.20
Deinococcus-Thermus	*Deinococcaceae*	*Deinococcus*	0.03	0.99	0.14
Actinobacteria	*Geodermatophilaceae*	*Blastococcus*	0.00	0.89	0.10
Actinobacteria	*Micrococcaceae*	*Arthrobacter*	0.01	0.87	0.10
Proteobacteria	*Burkholderiaceae*	*Massilia*	0.00	0.75	0.00
Actinobacteria	*Kineosporiaceae*	*Kineosporia*	0.00	0.62	0.00
Actinobacteria	*Kineosporiaceae*	*Kineococcus*	0.00	0.48	0.00
Proteobacteria	*Beijerinckiaceae*	*Methylobacterium*	0.00	0.49	0.06
Actinobacteria	*Microbacteriaceae*	*Marisediminicola*;ambig.	0.00	0.43	0.01
Actinobacteria	*Geodermatophilaceae*	*Modestobacter*;ambig.	0.01	0.47	0.07

Note. This is a subset of the differential abundance analysis output, sorted by magnitude of difference in abundance, and excluding operational taxonomic units (OTUs) lacking genus level taxonomy information. Multiple entries of the same genus means that multiple OTUs (approximately species level) within the genus met the criteria for inclusion in the table. OTU IDs and extended results are provided in Table S4.

4. Discussion

We have performed the first detailed characterization of the prokaryotic community in a landscape-scale dryland system comprising terrestrial, fluvial, and aeolian component—with focus on the soil surface microbiota. This is also one of only a few studies to identify the microbes present in the dryland Lake Eyre Basin of central Australia, which covers 1.14×10^6 km^2 (Habeck-Fardy & Nanson, 2014). Many Australian soil microbiology projects are indexed in the Biomes of Australian Soil Environments soil microbial diversity database (BASE; Bissett et al., 2016). However, studies using the published protocols involving homogenization of the top 10 cm of soil will be unsuitable for detailed evaluation of biocrust microbiota, which typically inhabit only the top few millimeters. A key distinguishing feature of this work is the focus on the soil surface, which is the interface between atmosphere and pedosphere. There is clear evidence that biocrust microbial communities are stratified at millimeter-scale (e.g., Garcia-Pichel et al., 2003; Elliott et al., 2014); however, it is still common in the biocrust literature to arbitrarily select the top 1 cm or sometimes more—often for pratical reasons. In this work we tried to more specifically target the organisms in the cohesive soil surface crust, which may be involved in adhesion of soil particles and ultimately contributing to landscape stability. Sampling in this way was found to be easier compared to taking an arbitrary depth selection, and we suggest that it is a preferable approach when objectives relate to understanding of the biocrust specifically.

Studies using high-throughput DNA sequencing with a focus on Australian biocrust communities specifically are rare (Abed et al., 2012; Chilton et al., 2018). While determining the microbial composition of soils was not our primary objective, community data in addition to those presented are made available in the NCBI Sequence Read Archive (project SRP150526) and supporting information Tables S2–S4. This is an important contribution as such data on drylands are lacking in the global literature (Ferrenberg et al., 2017), and it has been shown that Australian soils have unique microbial communities compared with other drylands (Eldridge et al., 2018). Our novel approach used landscape sampling combined with model based differential abundance analysis, enabling us to test and develop hypotheses about the ecology of biocrust organisms in drylands, particularly focusing on the implications of dispersal strategies for landscape stability and dust production.

4.1. Microbial Community of Biocrusts in a Dryland Ephemeral Lake Bed and Surrounding Dunes

Previous research on biocrust microbial communities in drylands is still rare in the literature (Ferrenberg et al., 2017) and has focused mainly on dune environments. We found that the dunes at our study site harbored typical biocrust communities with 59 % of sequences being of cyanobacterial origin, along with much of the remainder belonging to the phyla Actinobacteria, Acidobacteria, Chloroflexi, and Proteobacteria (Figure 4). The same phyla in similar proportions have previously been found in biocrusts of the Kalahari in Botswana (Elliott et al., 2014).

Dune and dune flank locations had very similar community structure, but were clearly distinct from the pan and the nebkha locations (Figure 4). It is normal to find different microbial communities in different situations so this result is as expected; however, the question lies in the nature and reason for the differences observed. Edaphic factors like grain size and soil chemistry are commonly linked to such observations; therefore, we interrogated the data for identification of links between measured variables and microbial community structure. The only link found was with the mass median diameter, and the correlation appeared to be driven by smaller particle size in pan sediments compared to the other areas sampled. It is therefore not clear whether particle size is driving some aspect of community selection, or if particle size is covariant with some other driving factor. The latter seems slightly more likely because we also included size fractions (Figure 2) in the model selection process, and no specific size fraction was found to be significantly related to microbial community structure. If particle size was driving (or influenced by) community structure then it would be expected that certain size classes would be better indicators than d50 for specific taxa in the community and therefore be selected in the model. Particle size distribution is likely to be related to a wide range of edaphic factors, which were not directly measured, including water availability and sediment chemistry, and these relations may explain why d50 was selected as a model constraint.

We suggest that different communities in linked compartments of this sedimentary system indicate the outcome of different selective pressures leading to establishment of organisms with different adaptations. Adaptations relating to soil adhesion are of particular relevance to landscape modification because they provide a potential mechanism for biotic control over a range of processes governing the properties and

movement of sediments. It is certain that biocrusts exert biotic control on landscape stability and state transitions (e.g., Bowker, 2007; Ferrenberg et al., 2017), but details are scarce especially regarding the relative roles of different taxa. Knowledge of which organisms contribute to structural properties of the soil, as presented in this paper, can help fill this knowledge gap and has wide ranging potential for applications in land management.

4.2. Wind Preferentially Lifts Certain Taxa from Biocrusts

We have found strong evidence that microbes are differentially liberated from the dryland soil surface by moderate wind (e.g., Figures 3 and 4; Tables 1 and 2). These results show that the adhesive properties of biocrust organisms vary, and importantly, they identify taxa which may contribute to particular geomorphic processes as a result of their biological adaptations. It is not possible to say at this stage whether such adaptations were selected because of their geomorphic influence, or whether geomorphic influence is incidental to some other selective pressure. Both mechanisms of selection seem likely and we expect that both occur.

It has previously been shown by Hu et al. (2003) that cyanobacterial abilities to stabilize sand grains in desert soils are largely in line with the amount of extracellular polymeric substance (EPS) produced and that the particular properties of EPS also play a role. For instance, *Microcoleus vaginatus* was recognized as a highly adhesive species, which is in agreement with our findings (e.g., Table 1) and general knowledge in the field. Since EPS is by definition extracellular, it is widely regarded in the biofilms literature to confer adhesive properties to the whole community (Flemming et al., 2007), and the same might be expected in soil surface biocrusts. It would appear from our results, however, that adhesiveness is not universally conferred to the whole community. Thus, some organisms may be adapted to avoid adhesion into the soil, and organisms adapted for promoting adhesiveness perhaps do not often achieve this without other related adaptations such as the production of long filaments.

Abed et al. (2012) have previously reported low levels of cyanobacteria in dust thought to be derived from biocrusts and saline lake sediments, proposing that their filamentous structure and EPS production may prevent their dispersal during deflation. Our data, which explicitly link source soil with derived aerosols, support this interpretation and extend it to other taxa. Many OTUs were found to resist entrainment (Table S4), including most Cyanobacteria, which have long been recognized for their stabilizing role in biocrusts (Belnap & Gillette, 1998). We found that sand dunes have a high proportion of taxa that resist wind erosion (Figure 4), thus sand dune surface communities are adapted in a way that promotes stability in the dune. This stabilizing effect of the microbiota can be regarded as ecosystem engineering, because it modifies the environment to provide the stable soil surface required for long-term biocrust survival. This kind of adaptation may also inhibit dispersal by the wind, limiting the ability of biocrusts to colonize new areas or regenerate after elimination, for example, as a result of overgrazing, because the regenerating inoculum must come from a local source (e.g., vegetative growth or transport by an animal). Possible difficulties for biocrusts to regenerate after extreme sustained disturbance is something we suggested in previous research as a risk (Elliott et al., 2014) and is supported by the present results which demonstrate the resistance of many biocrust taxa to becoming airborne.

The nebkha sites within the claypan were the only place where a high proportion of the microbiota was identified as being easily mobilized by wind (29 %; Figure 4). This was not a direct measurement but based upon taxa from the dune flank that were easily mobilized and measuring their abundance in the nebkha. We anticipate that a direct measurement on the nebkha sites would yield a higher proportion, but this would be extremely difficult to do because the nebkha morphology is incompatible with wind tunnel apparatus. It should also be noted that our techniques do not establish direction of transport in this system, therefore a proportion (possibly the majority) of the taxa mobilized from the dune flank by wind treatment are likely to have originated from the pan and nebkha sites. Indeed, some organisms may be adapted to exploit the whole system rather than a particular geographical compartment. The reason for a high proportion of wind-mobile biota on the nebkha may be partly related to physicochemical properties; however, our RDA model identified no variables that could explain the nebkha microbial community structure (Figure S4). A biological explanation may be that nebkha are inhabited by biocrust organisms that rely principally on aerial disperal, because they are adapted as primary colonizers of newly exposed niches. Such organisms would need to have the capacity for adhesion to establish a colony in the new niche but also an ability to disperse from the colony. This could be achieved by phenotypic switching which is a well-known phenomenon in biofilms with a variety of mechanisms available (e.g., Drenkard & Ausubel, 2002). Furthermore, biocrust organisms

adapted for aerial dispersal would need adaptations for survival in the air, such as small size and resistance to dessication and radiation. Alternatively, it is possible that the life strategy of some of these microbes is to be habitually nomadic—traveling in the atmosphere to visit soils and biocrusts from which they extract sustenance before releasing more propagules into the air to find the next place to settle briefly, and so on.

4.3. Microbial Dispersal and Landscape Stability

Biological adaptations for survival in fluvial-aeolian systems are likely to include mechanisms for modulating attachment to surfaces, which may have profound geomorphic consequences. Attachment to the soil will result in binding of particles, reducing the potential for dust emission both by increasing effective particle sizes and by physical entrapment of particles. While this is clearly advantageous to soil surface dwelling biocrust communities, it is also a potential hazard to be physically constrained in this way, because soils may be buried by dust or submerged under flood waters. Some organisms will overcome such hazards with adaptations for aquatic life or vegetative migration in the soil, and these properties are well known among cyanobacteria (e.g., Makhalanyane et al., 2015; Felde et al., 2018). Another likely adaptation is to promote destabilization of the biocrust to enable dispersal by the wind, which would lead to dust production and the transport of nutrients out of the soil. Once dispersed on the wind, microbes would have the opportunity to colonize new areas, thus ensuring survival even if the source area became inhospitable. A parallel situation is well documented in the biofilms literature which deals mainly with microbial cells living as attached communities in various aqueous environments such as medical devices and rivers. Even single-species biofilms exhibit both attachment and detachment phenotypes, triggered by genetic switches that respond to changing conditions (e.g., Drenkard & Ausubel, 2002). Macroscopic organisms also exhibit this behavior; for instance, scallops are normally regarded as sessile creatures, but they will swim away in response to environmental triggers (Caddy, 1968).

We propose that biocrust microbes in common with other organisms also have a variety of dispersal mechanisms and that their dispersal adaptations have geomorphic consequences such as influencing the particle size distribution and dust availability (e.g., by selectively trapping particles and producing aggregates). At least three distinct dispersal strategies are proposed which may be employed by biocrust organisms, each strategy having particular phenotypic features and related geomorphic potential (Table 3). While we suggest a typical niche associated with each dispersal strategy, we do not expect this to be exclusive. Rather, we suggest that these strategies coexist in each biocrust community, and the relative abundance of organisms exhibiting each phenotype will vary depending on the life history of each particular biocrust.

4.3.1. Fluvial Dispersal Strategy

Periodic cycles of wetting and drying are a common feature of the dryland soil surface which all biocrust organisms must adapt to in order to exploit occasional rainfall and dew. On pan surfaces there is a further requirement to survive or even thrive during floods as well as long periods of drought. When flood waters on pans subside, the sediment is rich in resources, and the aquatic microbiota deposited in large numbers have a numerical advantage that may hinder establishment of vegetatively or aerially dispersed microbes.

This is likely to have happened in the claypan, where the pioneer biocrust organisms may be mostly deposited aquatic species such as *Tychonema* spp. cyanobacteria that are ill-adapted for long-term survival out of water, but nevertheless condition the fresh sediment making it more hospitable for better adapted secondary colonizers. If these primary colonizers are adapted for fluvial dispersal via ephemeral lakes then their main task between flood events is to survive and exclude competitors until further floodwaters arrive, therefore they are likely to lie dormant unless activated by prolonged exposure to water. In terms of landscape stability they are expected to be an immediate benefit as floods subside due to the extensive production of biomass protecting and nourishing the fresh pan sediment; however, during dry times they may suffer erosion and are unlikely to have the capacity for repair.

4.3.2. Lateral Expansion Dispersal Strategy

Lateral expansion in biocrusts has been defined by Sorochkina et al., 2018 (Sorochkina et al., 2018; in the context of an experiment) as contiguous growth on the soil substrate. We adopt this terminology, which helpfully covers soil colonization through both vegetative growth and motility of the soil microbes—often it will not be obvious which mechanism is achieving the expansion. Lateral expansion dispersal strategy is implicitly assumed in the majority of biocrust literature, which holds that biocrusts are slow to establish and they gradually succeed to stronger forms (e.g., Belnap & Gillette, 1998). In the present work the sand dune biocrusts are a classic example of this standard view of biocrust development. Organisms relying on

Table 3
Summary of Hypothesized Dispersal Strategies for Biocrust Organisms and Their Possible Geomorphic Effects

Dispersal strategy	Niche	Likely phenotype	Geomorphic effect
Lateral expansion: e.g., *Microcoleus* spp. and *Wilmottia* spp. (Cyanobacteria); *Blastocatella* spp. (Acidobacteria)	Long-term stable soils: e.g., stabilized sand dune	oligotrophic mutualistic EPS production Can recover from localized disturbance Low water requirement	Strongly stabilize soil Suppress dust production Trapping dust Enhance soil fertility
Aerial: e.g., *Deinococcus* spp. (Deinococcus-Thermus); *Massilia* spp. (Proteobacteria); *Modestobacter* spp. (Actinobacteria)	Recently exposed soil and transient landscape features. Possibly active while airborne, e.g., nebkha	copiotrophic exploitative Limited recovery from localized disturbance Medium water requirement	Partially stabilize soil Promote moderate dust production including removal of soil nutrients
Fluvial: e.g., *Tychonema* spp. (Cyanobacteria)	Water bodies, flood plains, and pans e.g., claypan	Copiotrophic Excludes aerial invaders Poor ability to recover from localized disturbance High water requirement	Partially stabilize soil Suppress dust production Neutral soil fertility influence

Note. Example taxa for each mode of dispersal are given based on results from this study. Further candidate taxa can be identified from Table S4.

lateral expansion for dispersal are expected to be highly invested in maintaining a stable soil surface, which facilitates the establishment of long-term extensive colonies that are highly resilient to harsh environmental conditions. Sorochkina et al. (2018) recently showed in a greenhouse experiment that the lateral expansion rate of biocrusts under favorable conditions was in the order of up to 2 cm/month. In our field site and drylands generally such conditions are not met most of the time, so realistic rates in the environment are likely to be lower. Therefore, newly exposed niches resulting from flooding, land slips, or burial are unlikely to be colonized solely by lateral expansion which is a slow process (e.g., based on the typical flooding interval of 3 years for the claypan, lateral expansion can account for only about 1 m of biocrust lateral growth). Indeed during their experiment, Sorochkina et al. (2018) found that aeolian propagules colonized soil ahead of the laterally expanding biocrust even in a greenhouse which had some protection from airborne inocula.

Our data suggest that cyanobacteria belonging to the genus *Microcoleus* (among others) are likely candidates for lateral expansion as a main dispersal strategy (see Tables 1 and S4 for more), and this fits with prior observations (e.g., Sorochkina et al., 2018). Even so we do not suggest that these organisms lack the capacity for aeolian or fluvial dispersal, but we expect that they will be much less efficient at this—for instance, using these mechanisms over shorter distances or only as a consequence of disturbance. Less commonly recognized in the biocrust literature is that noncyanobacterial taxa may be part of the biocrust and contribute to its ecology and stability. Our results identify a wide range of such organisms, for example, *Blastocatella* species. The genus name *Blastocatella* means "budding small chain"—in reference to a strong tendency to form chains and larger aggregates as determined by Foesel et al. (2013) in their description of the new genus and the first described species of Acidobacteria subdivision 4 (*Blastocatella fastidiosa* isolated from semiarid savanna soil in Namibia). Chain and aggregate formation at the cellular level is consistent with our hypothesized properties for biocrust-forming organisms that use a vegetative dispersal strategy, as they are expected to enhance soil stability. Other properties of *Blastocatella* species identified by Foesel et al. (2013) include pigment production and oligotrophy, and they note that little is known of the ecophysiology of Acidobacteria in biocrusts and similar habitats. We suggest that *Blastocatella* species and related taxa have specific adaptations for life at the soil surface which promote the formation and stabilization of biocrusts in drylands.

Unlike pan surfaces, stabilized sand dunes do not experience wholesale disruption via flooding; therefore, succession can take place over long timescales and uncrusted sites exposed by localized disturbances can

likely be recolonized by vegetative growth from nearby areas or from beneath when crusts become buried (Elliott et al., 2014; Felde et al., 2018). It is known that biocrust biota can move vertically in the soil, enhancing their survival prospects by responding to environmental stimuli including water and light (Garcia-Pichel & Pringault, 2001). While burial depths exceeding 1 cm severely threaten survival of the biocrust organisms, shallower burial can be tolerated (Rao et al., 2012). Repeated biocrust burial followed by reestablishment of surface biocrusts results in the production of stratified fossil crust microhorizons in dryland sand soils, contributing to soil stability as a direct result of biocrust lateral expansion (Felde et al., 2018). In this work we have identified taxa which are likely to be contributing to that process, and therefore could be used as indicators of soil stability or as inoculants in interventions designed to enhance soil stability.

4.3.3. Aeolian Dispersal Strategy

Biocrusts may also be established from airborne inocula, and the nebkha biocrusts are most likely an example of this. Because strongly adhesive biocrust taxa are less likely to become airborne, biocrusts established from airborne sediments may lack the strength of colonially established biocrusts at least initially until more stabilizing taxa with capacity for lateral expansion move in (and possibly ultimately out-compete them). They must therefore rely on other stabilizing landscape features such as stones and plants, enabling them to settle without investing strongly in promoting landscape stability, although they probably do this incidentally. Taxa adapted for aerial dispersal must achieve high numbers in the atmosphere to be successful, thus they are likely to be R-strategists or copiotrophs that exploit islands of fertility to produce more airborne inocula. This means that although they have some capacity to stabilize soil, they may also contribute to dust production and export of nutrients from the soil.

Our data suggest that *Deinococcus*, *Massilia*, and *Modestobacter* species (among others) may be adapted for aeolian dispersal as part of their life cycle (Table 2), and these taxa have properties consistent with our hypothesized ecological strategies for airborne dispersed biocrust organisms (Table 3). *Deinococcus* species are well known for their remarkable ability to withstand dessication and intense radiation (Makarova et al., 2001). This genus has been found in desert soils before (e.g., Rainey et al., 2005; Chilton et al., 2018), and Li et al. (2012) detected *Deinococcus* species at low abundance in aerosols thought to be derived from biocrusts or saline lake sediments in Australia. According to Bergey's manual (Whitman, 2015), the natural habitat of *Deinococcus* species remains unknown. We suggest then that the habitat of this ancient lineage is in fact the biocrust top surface, and it is adapted for wind dispersal. *Modestobacter versicolor* may have a similar ecology. Isolated from topsoil dryland biocrusts, it is a moderately oligotrophic aerobic chemoheterotroph with radiation tolerance and capacity for nitrogen fixation (Reddy et al., 2007). Interestingly, Reddy et al. (2007) report that this species produces pigments (which are presumed to confer protection from UV light) only when under oligotrophy, which could be an adaptation for dispersal by air—since air is a more oligotrophic environment than the biocrust surface, and UV exposure would be greater during transit through the air. *Massilia* species have commonly been found in biocrusts, recognized for resilience and fast growth, they have recently been shown to respond rapidly to hydration in dryland soils (Aslam et al., 2016). With such ecologies *Deinococcus* species and other wind-dispersed biocrust species may serve a protective function to the biocrust and can also ensure that they quickly colonize any newly suitable soils and sediments arising from events such as land slips and animal disturbance. Airborne inocula may therefore play an important role in the stabilization of landscapes by initially protecting disturbed soils and preparing the way for secondary vegetative colonizers such as cyanobacteria. This idea could be tested by disturbance experiments and monitoring the succession of microbes, which we predict would begin with taxa such as *Deinococcus*, *Massilia*, and *Modestobacter*.

5. Conclusions

In conclusion, we have shown that biocrust taxa vary in their capacity to be mobilized by the wind and we have suggested that this is driven in part by ecological dispersal strategies which in turn determine the taxon potential to enhance or degrade landscape stability. We have shown that biocrust microbes are found in watercourses and proposed that some biocrust taxa are principally dispersed by fluvial deposition. Our results provide new evidence supporting the microbial role in landscape stability and suppression of dust production in drylands. By interpreting results from an ecological perspective, we provide a theoretical basis for predicting how microbes will influence landscape stability under different scenarios. Such predictions can be tested in future work, for instance, by monitoring establishment and succession in biocrusts over

time, in tandem with physical assessments. An ecological approach informed by microbiology can then be developed to help predict landscape responses to climate change and land use change and also to design mitigation strategies for maximizing soil stability.

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